DEVELOPMENT, SWARMING, COLONY ORPHANING AND FLY PARASITISM IN SUBTERRANEAN TERMITES, *Macrotermes gilvus* (Hagen) AND *Macrotermes carbonarius* (Hagen) (BLATTODEA: TERMITIDAE)

by

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PERKEMBANGAN, PENGERUMUNAN, PENYATIMAN KOLONI DAN PARASITISME LALAT DALAM ANAI-ANAI TANAH, *Macrotermes gilvus* (Hagen) dan *Macrotermes carbonarius* (Hagen) (BLATTODEA: TERMITIDAE)

ABSTRAK

Aspek biologi dan ekologi *Macrotermes gilvus* (Hagen) dan *Macrotermes carbonarius* (Hagen) seperti berikut: (1) kajian perkembangan kasta; (2) fenologi penerbangan dan mekanisme isolasi reproduktif; (3) impak penyatiman koloni lapangan; (4) parasitisme larva lalat difokuskan dalam kajian ini. Kajian ini memberi pemahaman mengenai tapak jalan perkembangan kasta anai-anai, biologi populasi, struktur pembiakan koloni dan ekologi komuniti.

Terdapat tiga peringkat larva and lima peringkat nimfa dikesan dalam perkembangan kasta perkerja minor/major dan reproduktif masing-masing. Peringkat larva pertama mengandungi kedua-dua jantan dan betina yang mempunyai saiz yang homogenus. Saiz dimorfisme seksual, di mana betina lebih kecil daripada jantan, berlaku pada peringkat larva kedua, peringkat larva ketiga dan peringkat pekerja. Askar minor dan major merupakan betina yang steril. Bukti gambaran dari peringkat larva keempat *M. carbonarius* ditunjukkan di mana individu tersebut menyerupai pekerja minor tetapi kurang pigmentasi dan mempunyai abdomen yang busung, dan rahang, meso- dan metanotum yang menyerupai pra-askar.

Reproduktif isolasi kronologi dipamerkan dalam dua simpatrik species, *M. gilvus* dan *M. carbonarius*. Penerbangan *M. gilvus* direkodkan sepanjang tujuh bulan, dari bulan Mac ke September, manakala, pengerumunan *M. carbonarius* berlaku dari bulan November ke Januari. Aktiviti pengerumuman *M. gilvus* dan *M. carbonarius* berlaku di

bawah tekanan atmosfera 1,005–1,011 hPa dan 1,006–1,010 hPa, masing-masing. Kebanyakan penerbangan *M. gilvus* berlaku pada hari hujan waktu subuh (0300-0430 jam), sedangkan, *M. carbonarius* mengelak daripada hari hujan pada waktu senja (1900-1910). Penerbangan *M. gilvus* berlaku dalam ambang suhu dan kelembapan relative (RH) antara 23 dan 26 °C, dan 83 dan 98% RH; *M. carbonarius* mengerumun antara 25 dan 30 °C, dan 72 dan 83% RH. Aktiviti penerbangan *M. gilvus* tertumpu pada bulan panas dan lembap dengan jumlah hujan bulanan tercatat 228 mm.

Daripada 38 koloni *M. gilvus* yang diyatimkan, 15 koloni (39.5%) didirikan semula. Dalam *M. carbonarius*, tiga koloni daripada 20 (15%) didirikan semula. Koloni yang didirikan diketuai oleh adultoids yang normal. Di koloni *M. gilvus* yang diyatimkan secara semulajadi, dijumpai multiple adultoid berpigmentasi normal tetapi dengan sepasang sayap yang terkoyah. Bilangan reproduktif mungkin berkurangan apabila masa berlalu. Kekatu *M. gilvus* berkemungkinan mengambil masa selama enam bulan untuk bertumbuh ke adultoid berfungsi, dan lebih daripada 12 bulan bagi kekatu *M. carbonarius*. Kehadiran kasta seksual pada masa penyatiman koloni tidak semestinya meningkatkan kadar penubuhan semula koloni. Didapati bahawa jumlah untuk penjajahan semula oleh anai-anai spesies lain adalah tinggi selepas kematian koloni *M. gilvus* (18.4%) atau *M. carbonarius* (30.0%).

Kapsul kepala askar-askar yang berbentuk kurang normal dan mandibelnya yang pendek biasanya dijumpai di koloni yatim. Satu species lalat baru ditemui, *Misotermes mindeni* Disney & Neoh (Diptera: Phoridae) dikenalpasti memparasit askar *M. gilvus*. Sementara itu, *Verticia fasciventris* Malloch (Diptera: Calliphoridae) pertama dilaporkan sebagai parasitoid dalaman askar *M. carbonarius*. Kedua-dua species lalat

mempamerkan cara pupariasi yang berbeza dan kurang agresif berbanding dengan askar yang sihat.

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ABSTRACT

Biological and ecological aspects of *Macrotermes gilvus* (Hagen) and *Macrotermes carbonarius* (Hagen) namely: (1) the caste development; (2) flight phenologies and reproductive isolation mechanisms; (3) the impact of orphaning in field colonies; (4) fly larva parasitism in both species were focused in this study. The present research provides insight into termite's caste developmental pathways, population biology, colony breeding structures and community ecology.

There were three larval instars and five nymphal instars detected in the development of minor/major workers and reproductive castes of both species. The first larval instars consisted of both males and females that displayed homogenous sizes. Size sexual dimorphism, in which females were smaller than males, occurred in second larval instars, third larval instars, and worker castes. Minor and major soldiers were sterile females. Pictorial evidence of fourth larval instar of *M. carbonarius* is presented herein; the individuals closely resembled those of minor workers but were poorly pigmented, having a distended abdomen, future presoldier-like mandibles, and a meso- and metanotum.

Chronological reproductive isolation was displayed in two sympatric species. Flights of *M. gilvus* were recorded over a remarkably long 7-month period from March to September, while swarming of *M. carbonarius* took place from November to January. Swarming events of *M. gilvus* and *M. carbonarius* occurred under atmospheric pressures

of 1,005–1,011 hPa and 1,006–1,010 hPa, respectively. Most flights of *M. gilvus* occurred on days with rain at dawn (0300-0430 hour), whereas *M. carbonarius* avoided rain at dusk (1900-1910). Flight activity of *M. gilvus* was correlated significantly with atmospheric pressure and rainfall. The threshold temperature and relative humidity (RH) of *M. gilvus* flights were between 23 and 26 °C and 83 and 98% RH; *M. carbonarius* swarmed between 25 and 30 °C and 72 and 83% RH.

Of the 38 orphaned colonies of *M. gilvus*, 15 colonies (39.5%) re-established. In *M. carbonarius*, three colonies out of 20 (15%) re-established. Re-established colonies were headed by normal adultoids. In naturally-orphaned colonies of *M. gilvus*, multiple adultoids with normal pigmentation but torn wings were found. The number of reproductives probably declines over time. It may take alates of *M. gilvus* six months to develop to functional adultoids, and up to 12 months for alates of *M. carbonarius*. The presence of sexual castes at the time of orphaning may not necessarily guarantee the success of colonies in re-establishing themselves as breeding colonies. A high prevalence of occupation of the mounds by other termite species was found, after the death of *M. gilvus* (18.4%) or *M. carbonarius* (30.0%) colonies.

Soldiers with abnormal round head capsule and small mandibles were found in orphaned colonies. A new fly species *Misotermes mindeni* Disney & Neoh (Diptera: Phoridae), as identified infecting the soldiers of *Macrotermes gilvus* (Hagen). While the Oriental Bengaliinae blow fly, *Verticia fasciventris* Malloch (Diptera: Calliphoridae) was reported for the first time as an internal parasitoid of the soldiers of *Macrotermes carbonarius* (Hagen). Both dipteran species demonstrated different approaches in larval pupation while parasitized soldiers were less aggressive compared to healthy soldiers.

CHAPTER ONE

INTRODUCTION

Termites, or 'white ant' in layman's term, are infamous for the damage they cause to wooden and building structural damages in agricultural, urban area and cultural heritage (Pearce 1997, Korb 2007). Recently, termites (*Coptotermes formosanus* Shiraki) have been implicated in the tumble of floodwalls consequent upon Katrina and Rita hurricanes in New Orleans, and over 1,800 people lost their lives (Henderson 2008).

Annual damage caused by termites from 2005 was estimated at US$ 50 billion worldwide: with United States alone in 1994, approximately US$ 11 billion was spent in termite management (Wiseman and Eggleton 1994, Su 2002a,b, Korb 2007). In Malaysia, an estimated RM50 million is invested annually on termite control. The total repair cost due to termite damages is believably about 3–4 times higher than the total cost of termite management (Lee 2002, Lee 2007).

Termites are found predominantly in the tropical and subtropical regions (close to the equator), which cover 70% of the world (Lee 2007). However, the distributions of some termite species reportedly have extended to the cool zones (Eggleton 1999). To date, of over 2,600 described species, comprising a total of 281 genera (Kambhampati and Eggleton 2000), only about 83 species are identified as wooden and building structural pest (Su and Scheffrahn 2000). In Malaysia, damages caused by 12 species of subterranean termites (seven genera: *Coptotermes*, *Macrotermes*, *Microtermes*, *Globitermes*, *Odontotermes*, *Schedorhinotermes* and *Microcerotermes*) are encountered in forestry, agricultural and buildings, particularly in suburbia and rural area (Kirton and Wong 2001, Kirton and Azmi 2005, Lee et al. 2007).

Macrotermes, a mound-building pest genus, is gaining notoriety as a secondary structural pest that becomes active once the dominant *Coptotermes* species are suppressed or eliminated from buildings by baiting (Lee et al. 2007). In addition, *Macrotermes* species are infamous for their damage to field crops, such as sugar cane, and to wooden structures (Harris 1969, Roonwal 1970, Cowie et al. 1989). Managing *Macrotermes* infestations is more complex than dealing with those of *Coptotermes* (Lee 2002, Yudin 2002, Lee et al. 2007). To date, the infestation can be controlled only by chemical spraying; paper-based baits are ineffective against these genera, possibly due to lack of palatability and biological variation (e.g., caste developmental pathway) of the species (Ngee et al. 2004b, Lee et al. 2007).

Information on biological and ecological aspects about *Macrotermes* from Southeast Asia, particularly *Macrotermes gilvus* (Hagen) and *Macrotermes carbonarius* (Hagen) is fragmentary. The present work focuses herein

(1) the caste developmental pathways and provided detailed biometric descriptors of *M. gilvus* and *M. carbonarius*.

(2) flight phenologies, flight behaviours and mechanisms reproduction isolation of two sympatric termite species, *M. gilvus* and *M. carbonarius*.

(3) the impact of orphaning on field colonies of *M. gilvus* and *M. carbonarius*.

(4) the phenomena of dipteran larva-parasitism in *M. gilvus* and *M. carbonarius*.

CHAPTER TWO

LITERATURE REVIEW

2.1 Termites

Termites are believed to exist on the earth before any other social insects, as evidenced by the oldest described fossil termite, *Meiatermes bertrani* Lacasa-Ruiz & Martinez-DelClòs (family Hodotermitidae) found in Spain which dating to the Cretaceous (130 million years ago) (Thorne et al. 2000). However, the studies of fossils of petrified forests in Arizona suggest that termites existed in the Permian (220 million years ago) (Pearce 1997).

Termites share the same basal lineage with cockroaches (Blattodea) and mantids (Mantodea), which form a natural assemblage known as the Dictyoptera. The evidences from phylogenetic studies and morphological studies strongly suggested that termites are eusocial cockroaches. Termites are now nested within the cockroaches (family Blattodea) (Inward et al. 2007) by assigning a new epifamily Termitoidae for the termites and Cryptocercoidae for the sister group of the termite, *Cryptocercus* (woodroaches) (Eggleton et al. 2007). It indicated that termites might have evolved from a single 'social cockroach' species then diversified into a number of termite families. However, the lineage is somewhat challenged by Thorne (1990), Thorne and Carpenter (1990), and Kambhampati (1995) due to the distinct of life history and social behaviours between termites and cockroaches.

Generally, termites are classified into three main groups based on habitat, such as drywood termites (e.g., family Kalotermitidae), dampwood termites (e.g., family Hodotermitidae, Termopsidae) and subterranean termites (e.g., family Termitidae,

Rhinotermitidae). Drywood termites are usually found inside wood which contain low levels of moisture and always cause timber and wooden structural damages. They are non-soil-dependent species. Faecal pellets are always found near the termite exit holes in infested wood. Dampwood termites usually feed on decayed and high moisture content wood, for example old tree stumps and rotting logs.

Subterranean termites are highly dependent on soil and soil moisture for survival. They construct shelter tubes during the foraging process to prevent desiccation. Subterranean termites are the most destructive insect pest worldwide compare to those of drywood termites and dampwood termites.

Based on feeding types, mandible morphology and gut content, termites can be divided into, (1) soil-feeders – ingested material highly contents soil organic matter and silica; (2) soil/wood interface-feeders – termites feed on highly decayed soil-like wood; (3) wood-feeders – termites feed on wood and woody litter such as dead branches; (4) litter-foragers – termites forage on leaves and woody litter and stored their food in the nest; (5) grass-feeders – termites feed on dry grass and take back to the nest (Bignell and Eggleton 2000). However, some overlaps of feeding types often occur under unfavorable environmental conditions.

2.2 Fungus-growing termites (subfamily Macrotermitinae)

Fungus-growing termites (subfamily Macrotermitinae) are broadly distributed throughout the Palaeotropics: from the tropical rain forests to savannahs, but are not recorded from the Neotropics (i.e., Central and South America) and Australasia (Roonwal 1970, Wood and Sands 1978, Bignell and Eggleton 2000, Aenan and Eggleton 2005). They show mixed primitive and advanced features. Like other subfamilies of

higher termites, they lack of intestinal flagellates and share the same forked developmental pathway (see Figure 2.1). However, intestinal structure is relatively similar with those of lower termites (Roisin 2000).

The main four genera (i.e., *Hypotermes*, *Microtermes*, *Macrotermes*, *Odontotermes*) predominantly distribute in Southeast Asia (Tho 1992). However, *Hypotermes* and *Microtermes* are absent from Borneo, Celebes and the Philippines. Two possible explanations are the two genera dispersed much later after sea level rising and inundated the Sunda shelf or are poorly represented in the region (Tho 1992).

The subfamily Macrotermitinae comprises of approximately 330 species, covering 14 genera, and in the genus *Macrotermes* alone consists of 47 species (Kambhampati and Eggleton 2000). Aanen and Eggleton (2005) noted that *Macrotermes* originate from African rain forest and later invaded savannahs, Asia and the Madagascar. Based on molecular divergence estimates, *Macrotermes* is estimated to disperse to Asia in the early Tertiary, periods during humid climate; while to savannahs during the Miocene (Brandl et al. 2007).

The fungus-growing termites are generally detrivores, feeding mainly on dead wood, dead grass, dung and roots of dead or living plants. They are known to cultivate a symbiotic fungus (genus *Termitomyces*) in mycelial stage as round and white conidia on the fungus comb inside their colonies. The fungus combs are built from variation plant materials: from dead or green leaves, and dry wood, grass stalks and roots depend on their diet (Rouland-Lefevre 2000). In a more recent discovery, the first fossil fungus combs was extracted from 7-million-year-old continental sandstone (Chad basin) in N'Djamena (Chad) (Duringer et al. 2006).

2.2.1 *Macrotermes gilvus*

Macrotermes gilvus is widely disseminated in Southeast Asia, from Myanmar to Indonesia, and the Philippines and contain about nine subspecies which vary in ecological and biological aspects (Roonwal 1970). It usually present in the lowland of altitude range up to 160 m above sea level, particularly in rural and suburbia (i.e., parks and gardens) (Tho 1992). *Macrotermes gilvus* soldiers (Figure 2.1A) are immediately distinguished from all other *Macrotermes* by its anterior region of the hyaline tip of the labrum broadly conical, whereas the others, e.g., *Macrotermes carbonarius* (Hagen), have a trilobed hyaline tip. An estimated 106,000 ± 78,000 termite individuals populate in one colony with the ratio of worker to soldiers of 7:1 (Subekti and Nandika 2009).

Macrotermes gilvus is a common mound-building termite. The species builds conical earthen mound and range from 0.5–10.0 m and 0.28–2.10 m in diameter and height, respectively. The location of royal chamber is reportedly shifted to the upper part of one mound over time (Inoue et al. 1997). Despite of sibling relationship, the inner structure of *M. gilvus* mound and ways of storing plant litter in one mound were partially different from those of African Macrotermitinae (see Kalshoven 1956a,b).

In the Philippines, foraging populations of *M. gilvus* were estimated range from 25,000 to 46,000 foragers and foraging territory range about 124 to 350 m^2 (Acda 2004b). Ngee et al. (2004a) tested 15 Malaysian wood species and 14 Japanese wood species against field colonies of *M. gilvus*. The authors reported that *M. gilvus* show a high food preference on rubber wood (*Hevea brasiliensis* Muell. Arg.) with wood consumption rate can reach up to 2.3 kg per month (Acda 2004b). Acda (2003, 2004a) noted that *M. gilvus* is physical disturbance and temperature sensitive. The species usually abandoned infested wood when disturbed or when ambient temperature rises.

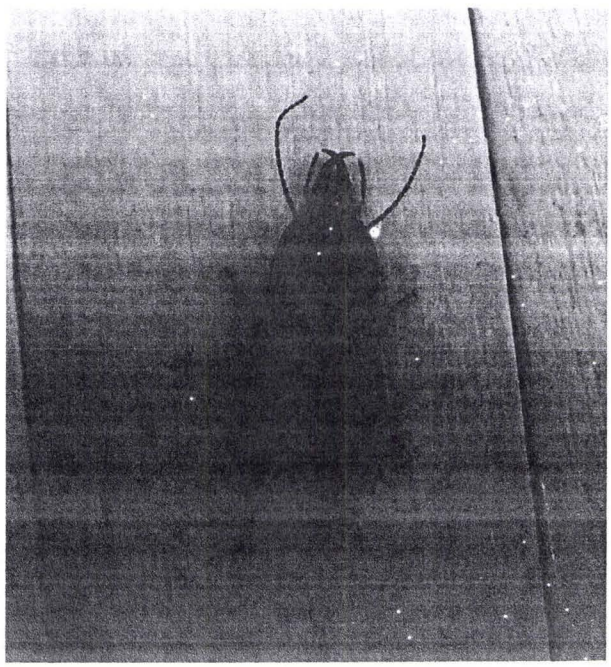
2.2.2 *Macrotermes carbonarius*

Macrotermes carbonarius is an abundant fungus-culturing termite species in Southeast Asia, found mainly in Thailand, Cambodia, the Malay Peninsula and Borneo (Roonwal 1970). The species is mainly located in lowland forest, agricultural and rural areas (Abe 1979, Abe and Matsumoto 1979, Tho 1992). It differs from other *Macrotermes* by it's heavily chitinized from orange-red to black body and head capsule (Figure 2.1B). The population in one given colony of *M. carbonarius* is approximately 88,500 termite individuals with the ratio of workers to soldiers is 6.4:1 and the ratio of neuter castes to larvae is 1.4:1 (Matsumoto 1976).

The species builds large subconical epigeal mound which can reach up to 4 m in height and 5 m in diameter (Roonwal 1970). The mound is made of large proportion of clay, particularly the brood chamber (McComie and Dhanarajan 1993). Despite lacking of air passage, the mound has several adaptive constructions: (1) thick wall as an insulator (Yamada et al. 2009) in maintaining the brood chamber temperature at 29°C (McComie and Dhanarajan 1990), and (2) the construction of numerous comb chambers allows inner gas exchange (Yamada et al. 2009).

Macrotermes carbonarius usually forages for food on open ground, by constructing pavement track on the ground (Sugio 1995). The underground passage systems only are connected with 4–10 major tracks with total length of between 33.8 and 112.8 m (Inoue et al. 2001).

(A)



(B)

Figure 2.1: Major soldier. (A) *M. gilvus*; (B) *M. carbonarius*

2.3 Economic importance of Macrotermitinae

Macrotermitines is infamous for their damage to field crops, such as sugar cane, wheat, tea, maize, coconut, etc., (Harris 1969, Mitchell 2002, Rajagopal 2002, Zhung and Liu 2002) and to young and exotic trees (*Eucalyptus* spp.) in Africa and India (Cowie et al. 1989). The termites attack plants by cutting and destroying the whole root system (for large species) or hollowing into the root and causing inner damage to the plants (for smaller species) (Mitchell 2002). Particularly, stressed plants, such as under disease attack (i.e., fungal attack, microbial infection), insufficient watering or drought, physical damages (e.g., fire, improper tree branch trimming) are generally the most susceptible to termite attack (Perry et al. 1985).

Other macrotermitines, *Odontotermes formosanus* (Shiraki) and *Macrotermes barneyi* Light (Macrotermitinae) are responsible for more than 90% of river dykes and reservoir dams collapsed and 60% of transportation structures in southern China (Zhung and Liu 2002). In South Africa, the fungus-growing termites, such as *Odontotermes badius* (Havilandi), *Odontotermes latericius* (Havilandi) and *Macrotermes natalensis* (Havilandi) cause 87%, 3% and 9% of building infestations, respectively (Mitchell 2002).

Macrotermes gilvus can be readily found in perimeter buildings, particularly in suburbia and rural areas (Lee et al. 2007). It is reported as a second destructive termite group in attacking building structures, which account for 13% of all infestation in semi-urban areas (Peninsular Malaysia) (Kirton and Azmi 2005), covering 6% in Northern Peninsular Malaysia (Lee et al. 2007). Acda (2004a) reported that *M. gilvus* is probably the second most destructive pest after *Coptotermes gestroi* (Wasmann) (previously *C. vastator*) in the Philippines and causes serious damages to wooden fences and posts,

utility poles and lumber (Acda 2003). Furthermore, the incident of *M. gilvus* as a secondary structural pest infesting the premises which had been previously treated for *Coptotermes* spp. using hexaflumuron baits is relatively high (4.9%) (Lee et al. 2007). *Macrotermes gilvus* can be found in the premises as early as two months after the suppression or elimination of the predominant *Coptotermes*.

2.4 Termites as beneficial insects

Despite of termites' well-established role as destructive pest, termites are considered as the most beneficial insect groups in natural ecosystems (e.g., Zungoli and Benson 2004). Termites are typical agro-ecosystem engineers (Dangerfield et al. 1998). They modify (1) soil porosity, water holding capacity and under certain conditions affect infiltration rates. These may attribute to the behaviour of termites in repacking and cementing soil during mound building or the construction of subterranean galleries (Holt and Lepage 2000), (2) soil quality and nutrient such as pH, water content, organic carbon and nitrogen (Donovan et al. 2001). Termites, particularly in soil feeding termites, use nutrient rich salivary secretions and faecal materials as cementing agents, (3) soil composition through relocation of soil particles for mound construction (McComie and Dhanarajan 1993, Jouquet et al. 2003) and etc. The overall effect of termite activities may influence the composition and spatial arrangement of organism diversity (Black and Okwakol 1997, Dangerfield et al. 1998, Traoré et al. 2008). For example, in a savannah, *Macrotermes* termitaria were found to have significantly higher tree density, and modify tree species distribution and diversity in one locality (Menaut et al. 1995).

Termites are exclusively cellulose-based feeder, with a wide array of food ranging from the tissues of living plants, wood, and roots, plant litter and humus in varying degree of decay. Termites are essential for the energy flow and recycling of nutrients in the natural environment (e.g., Martius 1994, Black and Okwakol 1997). Among termites, Macrotermitines are well represented in the role as Macrotermitines transformed 1,300–1,500 kg ha^{-1} of plant litter into fungus combs (Collins 1981).

Termites are also consumed as food source to other insects (e.g., driver ants: Schöning 2007), animals (e.g., chimpazees: Collins and McGrew 1985), as well as humans. For example, winged termites of *Macrotermes* are important protein source in many other parts of Nigeria and Africa (Agbidye et al. 2009). Termites have been reported to contain essential nutrients to the human diet (Kinyuru et al. 2009). In Australia Northern Territory, huge termite mounds can serve as tourist attraction (Lee 2007). In Malaysia and Singapore, the culture of worshipping termite mounds is widely practiced, especially by local Chinese and Indian communities (see Lee 1999).

2.5 Castes of termites

Termite societies show three basic characteristics which differ from that of the social Hymenoptera: (1) termites undergo incomplete metamorphosis (hemimetabolous) (Krishna 1969). (2) termite societies contain males and females which share social tasks equally (Krishna 1969) whereas males almost play no role in the social organization of hymenopteran. (3) termites are diploid, while Hymenoptera are haplodiploidy (Korb 2007).

A termite colony is basically comprised of immature individuals, workers, soldiers, alates and reproductives. Immature individuals are distinguished as nymphs

which possess a pair of wing buds and potentially develop into winged alates; while larvae (the term larvae is not equivalent to the term used for holometabolous insects) are lack of wing buds and display several moulting with little morphological changes to either workers or soldiers (Pearce 1997).

Workers and soldiers are wingless, blind (except Hodotermitidae), and sterile which the sex apparatuses appear in incipient stages and cannot be determined by the structure of the posterior abdominal sternites (except Mastotermitidae, Hodotermitidae, Rhinotermitidae and Kalotermitidae) (Weesner 1969a, Zimet and Stuart 1982). Sexual polymorphism always present in the family Termitidae. For example, there are two types of sterile castes, which are major (male) and minor (female) in the subfamily Macrotermitinae; and three types of sterile castes – major (female), intermediate (female) and minor (male) in the subfamily Nasutitermitinae (Miura et al. 1998, Roisin 2000).

Nymphs moult into sexually mature, highly pigmented and winged adult male and female (alates). Alates are produced on a seasonal basis and are potential founders of new colonies (Pearce 1997). Female winged termites are always larger than those of males (Noirot 1969, Roonwal 1975, Thorne 1983) as females under consistent selection for high fertility (Boomsma et al. 2005, Husseneder and Simms 2008). However, some exceptional cases were reported in genus *Microcerotermes*, *Nasutitermes*, *Termes*, *Cubitermes* and *Amitermes*, which the males and females are the same size (Noirot 1969).

Male and female alates shed their wings and form pairs soon after swarming activity. The pairs burrow into soil, or wood (Kalotermitidae) and commence breeding in a colony. The differentiation of replacement reproductives occurs if primary

reproductive(s) being removed, unhealthy or die. However, the potential of the development of replacement reproductives within one colony is highly variable across species (see section 2.7).

An individual that possesses an intermediate characteristic, by exhibiting a combination of two or more features of another caste (i.e., nymph-soldier, worker-soldier) is termed intercaste (Weesner 1969a). The individual always play a lesser role in one termite society. The occurrence of intercaste is common in primitive termites (Adamson 1940, Koshikawa et al. 2004) rather than higher family of termites (Termitidae) (Lefeuve and Thorne 1984, Roisin and Pasteels 1986a, Hojo et al. 2004). Intercastes occur naturally in some colonies [e.g., *Nasutitermes guayanae* (Holmgren) and *Microcerotermes arboreus* Emerson: Adamson 1940; *Nasutitermes lujae* (Wasmann) and *Nasutitermes columbicus* (Holmgren): Lefeuve and Thorne 1984]; or may result from colony orphaning (Roisin and Pasteels 1986a), parasitism (Roisin 2000), or juvenile hormone induction (e.g., Scharf et al. 2003, Hrdý et al. 2006, Habibpour et al. 2007).

2.5.1 Caste development pathways

The postembryonic development of higher termites is highly variable compared to that of lower termites (Noirot 1969). Caste systems have been extensively studied in three families, Kalotermitidae, Rhinotermidae (lower termites), and Termitidae (higher termites), which exhibit linear and forked developmental pathways (the latter two family except *Prorhinotermes*), respectively. The central (linear) developmental pathway (Figure 2.2A) displays that the first larval instar undergo seven successive moultings to become alates in Kalotermitidae (Roisin 2000). The worker force consists of late larvae,

nymphs, and pseudergates (so called helpers or false workers), which possess a pair of reduced wing buds, are derived from a unique regressive moults from the sexual castes (Noirot 1969). The development is highly flexible in which pseudergates may undergo a combination of progressive, stationary, and regressive moults to become nymph, neotenic reproductives or soldier (Roisin 2000).

The developmental pathway of *Prorhinotermes simplex* (Hagen) (family Rhinotermitidae) shows similarity to that of the Kalotermitidae (Miller 1942). The larvae go through six moults to give rise to the alates. In contrast, the development of the Rhinotermitidae in general [e.g., *Reticulitermes* (Buchli 1958, Takematsu 1992), *Coptotermes* (Roy-Noël 1968, Roisin and Lenz 1999)] exhibits an early divergence between neuter and sexual castes during the second larval instars (Figure 2.2B).

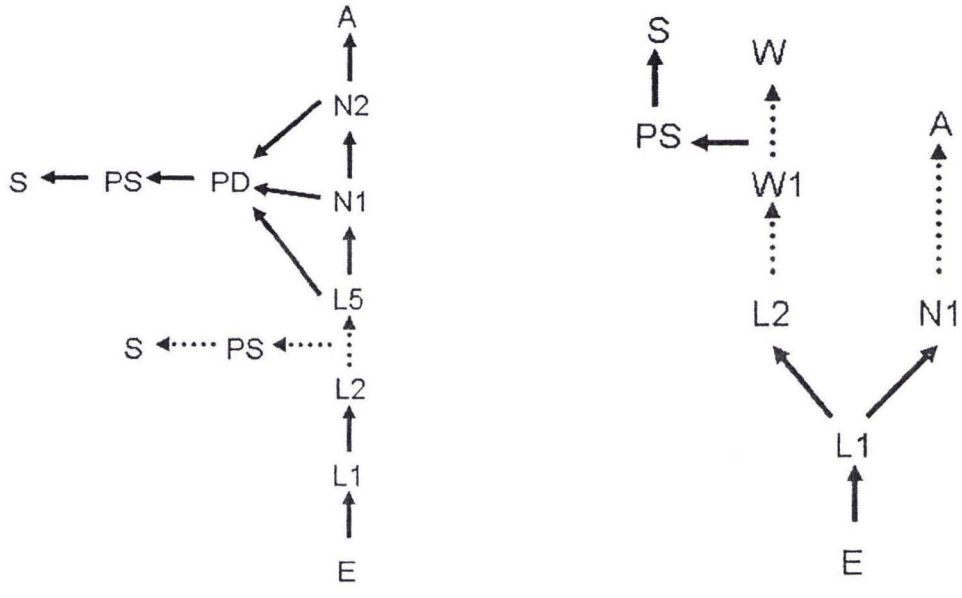
The forked developmental pathway (Figure 2.2B) separates two developmental lines (sexual and neuter) at the first larval moult. In Termitidae, the developmental pathway of the sexuals (alates and nymphs) is constant (Noirot 1969). The alates go through one undifferentiated larval instars and followed by five immature nymphal instars. In contrast, the developmental pathway of neuter castes is genera-specific. Some species have two (e.g., the Nasutitermitinae) or three larval instars (e.g., Macrotermitinae and the Rhinotermitinae) followed by one or a couple of worker instars (Noirot 1969, Roisin 2000).

Two common characteristics display in family Termitidae. First, workers often show sexual dimorphism, in which females are larger than males in many species, as observed in Nasutitermitinae (Roisin 2000) and Termitinae (Stewart and Zalucki 2006). However, it is the opposite in subfamily Macrotermitinae (Okot-Kotber 1981). Second, workers of the same sex give rise to soldiers, e.g., all males in Nasutitermitinae (Noirot

1955, Miura et al. 1998, Roisin 2000) and females in *Microcerotermes* (Roisin 1990, Stewart and Zalucki 2006) and the Macrotermitinae (Noirot 1955, Okot-Kotber 1981). The post-embryonic developmental pathway of the Hodotermitidae shows a great similarity to those of the Termitidae (Roisin 2000).

In Termopsidae, termopsids go through seven moults to give rise to alates, and soldier caste forks at the sixth moult in the reproductive line. The colonies of all termopsid genera are commonly headed by reproductive soldier(s) to commence breeding (Lenz 1985, Koshikawa et al. 2004).

Watson (1971) proposed that *Mastotermes darwiniensis* Froggatt (Mastotermitidae), the sister-group of all other termites features five larval stages followed by several sizes of pseudergates. There are three nymphal stages which derive from the intermediate to large size of pseudergates. The large pseudergates potentially develop into neotenics and presoldier. However, the developmental scheme was re-examined and claimed that the second larval instars and onwards, which covered with fine hair on body were identified as nymphs, while one with sparse hair as larvae (Watson et al. 1977).



(A) (B)

Figure 2.2: Central developmental pathway of Kalotermitidae (A) and Forked developmental pathway of Rhinotermitidae and Termitidae (B). E, egg; L1-L5, larval instars; N1-N2, nymphal instars; A, alates; PS, presoldier; PD, pseudergates; S, soldier; W, worker. Modified from Roisin (2000)

2.6 Colony foundation and swarming

Colony splitting (budding) by producing neotenic reproductives and synchronized release of alates (swarming) from parental colony are main strategies for colony foundation and species dispersion (Lepage and Darlington 2000), especially in eusocial Hymenoptera and termites (Wilson 1971). The former is always referred as inbreeding reproduction, which happens in polycalic colony [*Nasutitermes princeps* (Desneux): Roisin and Pasteels 1986b] or upon the death of primary queen and/or king [*Coptotermes lacteus* (Froggatt): Lenz et al. 1988]. In *Reticulitermes speratus* (Kolbe), unmated females can form colonies through asexual reproduction (parthenogenesis) (Matsuura and Nishida 2001, Matsuura et al. 2009). Swarming is the commonest reproductive strategy in one colony. It is often constraint to abiotic (extrinsic) (Table

2.2) and biotic (intrinsic) factors or in combinations (Nutting 1969). It is completed by winged adults (alates) which are produced seasonally in one mature colony.

There are three basic sequences of the reproductive process in swarming. First, dispersion begins when alates become gregarious, with workers and soldiers segregating in superficial or special chamber of the nest and disperse from the parental colony. This followed by pair calling, pairing, dealation and tandem running which generally take place after flight. Second, mating which occurs after the pair selects their nesting site. Third, colony foundation take place when the pair burrow into wood (wood-dwelling termite) or soil (subterranean termite) and the development of the colony starts once the first batch of eggs and larvae present (Nutting 1969).

The flight season varies with termite species and location. In temperate regions, flight activity usually is restricted to rainfall events within the warmer months (Nutting 1969, Dunn et al. 2007); whereas many flights coincide with the main rainy periods in the tropic (e.g., *Macrotermes*) (Darlington 1986) and in rainfall restricted region such as Sahara desert (e.g., *Acanthotermes*) (Clément 1956). In contrast, most of tropical lower termites (Rhinotermitidae and Kalotermitidae) swarm throughout the year and some sporadic small flights also occurred beyond the peak season (Wilkinson 1962, Ferraz and Cancello 2001, Neoh and Lee 2009b).

2.6.1 Abiotic factors

The initiation and synchronization of insect flight activity always related to climatic factors, especially temperature and rainfall. Temperature restricts flights by influencing insect physiological activity. Most insects show high level reproduction activity and abundance in warm environment (Corbet 1999, Kaspari et al. 2001). The fact is in agreement with observations on *C. gestroi* in Brazil (Ferraz and Cancello 2001)

and peninsular Malaysia, which swarming activities occur throughout the year (Neoh and Lee 2009b).

Rainfall and moisture condition are favored for flight as (1) high humidity prevent small athropods from desiccation (Kaspari 1993), (2) rainfall promotes vegetation growth by increasing food availability for the plant/plant-litter based feeding organisms (Pearce 1997, Kaspari et al. 2000), (3) rainfall softens the soil and allowing soil excavation, especially for subterranean organisms (Nutting 1969, Hölldobler and Wilson 1990). However, heavy rainfall may be detrimental to the alate flight activity (see Chapter Four) as well as foraging activity (Pearce 1997).

Apart from the above, light intensity, wind velocity, atmospheric pressure, and electric properties of the atmosphere may also hinder flight activity (Nutting 1969). In addition, a few studies documented a number of environmental factors. For example, (1) food availability as well as accessibility of resources by termites and food competition may affect sexual castes production (Henderson 1996, Korb and Linsenmair 2001, Korb and Lenz 2004, Korb and Schmidinger 2004). (2) Predation pressure may influence the time of flight and flight patterns (Robinson 1996). An individual factor might influence the decision for alates to fly, or certain combinations of factors might affect their flight activity (Brian 1965, Nutting 1969).

2.6.2 Biotic factors

Extreme environmental conditions constrain flight activity, particularly in arthropods which always encounter the risk of desiccation under unfavorable thermal conditions. Thereby, physiological advances (Saastamoinen and Hanski 2008) and nutritional requirements (Wanner et al. 2006) play important roles in sustaining insect

fitness for active flight. Gurevitz et al. (2006) documented that sex and adult age have strong effect on flight initiation of the blood-sucking bug, *Triatoma infestans* Klug.

The production and development of alates in one termite colony is under colony-level constraint, e.g., colony stage, colony size, pheromone which are exchanged through grooming and trophallaxis and integration of other termite caste. Generally, termite colonies produce alates after three to four years (*Macrotermes jeanneli* Grassé: Leuthold et al. 2004), colony size reaches approximately 0.6–1.7 million adult sterile castes (*Macrotermes subhyalinus* Rambur: Darlington 1990). Worker force is needed in constructing the exodus holes of alates and determines the ideal environmental condition to issuing alates. Soldiers usually position within the exits or outside of dispersal holes to protect alates from predators' attack (Nutting 1969).

Table 2.1: Effects of environmental variables on termite flight activity and flight patterns in different regions.

Species	Environmental variables				Flight pattern			References
	Temp. (°C)	R.H. (%)	Rainfall (mm)	Wind velocity (m/s)	Month & region	Time	Distance (m)	
Macrotermitinae								
Macrotermes natalensis	17–19	39–90	>5	Windless	Sept.–Dec. South Africa	1730–1820	N.A.	Mitchell 2008
Macrotermes gilvus	23–26	83–98	88–228 (month)	Windless	Mar. –Sept. Penang, Malaysia	0300–0430	≈ 100	Chapter Four
Macrotermes carbonarius	25–30	72–85	146 (month)	Windless	Nov. –Jan. Penang, Malaysia	1900–1910	≈ 30	Chapter Four
Marcrotermes barneyi	20–28	80–85	Rain	Windless	Apr. –July, China	2300–0600 (esp. 0400)	N.A.	Dai and Dai 2000, Tong 2004
Odontotermes formosanus	25.2	92.3	Rain	0.3	Apr.–June Guandong, Southern China	1830–1930	120–743	Hu et al. 2007
Termitinae								
Microcerotermes championi	22–37	80–84	0–58	N.A.	June–Aug. Lahore, Pakistan	1930–2100	N.A.	Rasib 2007

Nasutitermtinae								
Trinervitermes spp.	65–70	>90	Heavy rain	N.A.	Apr. Samaru, Nigeria	2300 until dawn	N.A.	Sand 1965
Rhinotermitinae								
Coptotermes gestroi	27–28	83–84	51–250 (month)	N.A.	Throughout year Penang, Malaysia	N.A.	N.A.	Neoh and Lee 2009b
Coptotermes gestroi (C. *havilandi*)	17–31	35–90	0–15	N.A.	Throughout year São Paulo, Brazil	1800–1900	N.A.	Costa-Leonardo and Barsotti 1998, Ferraz and Cancello 2001
Kalotermitidae								
Paraneotermes simplicicornis	23–32	36–99	<32	N.A.	May–Sept. Tucson, Arizona	During dusk	N.A.	Nutting 1966

N.A., not available

2.6.3 Reproductive isolation

The sympatric coexistence of sibling or sister species in one habitat may promote interspecific hybridization. For example, alates of *M. subhyalinus* and *M. michaelseni* which are predominant in Kenya successfully formed mixed pair in laboratory condition (Lepage and Darlington 2000). However, hybrids appear to be infertile in most cases due to hybrid dysgenesis syndromes (Hägele 1999).

Swarming behaviour is a key mechanism of reproductive isolation in termite (Bouillon 1981). Several strategies are identified to avoid hybridization of congeneric species and its associated costs (Stiles 1975). For sympatric species which show simultaneous flight, sexual isolation might be governed by species-specific sexual communication signals (volatile or contact pheromone) to avoid confusion and cross-breeding (Peppuy et al. 2004). This is the case of the subtropical sympatric species, *Macrotermes annandalei* (Silvestri) and *M. barneyi* which secrete species-specific sex pheromone from tergites 6–10 and tergites 5–10, respectively (Peppuy et al. 2004).

In some cases, sympatric termite species that respond to the same sexual communication signals might exhibit disparate flight patterns, or so called chronological reproductive isolation (Wood 1981, Hölldobler and Bartz 1985). Several studies have shown that species within genera may display staggered flight patterns, within a particular day (day flyer and night flyer) (Darlington 1986), or across months (Chapter Four). The phenomena were shown in *Pseudacanthotermes spiniger* (Sjöestedt) and *Pseudacanthotermes militaris* (Hagen) (Bordereau et al. 1993), *Reticulitermes santonensis* Feytaud and *Reticulitermes lucifugus grassei* Clément (Clément 1982), and possibly *M. subhyalinus* and *M. michaelseni* (Lepage and Darlington 2000) which use the same sex pheromone, dodecatrienol, and fly at disparate periods.

Reproductive isolation through behavioural mechanisms was reported in seven *Microtermes* species (Wood 1981). These are (1) pair forming occurs on the ground or during flight. (2) Calling behaviour – females position upside down on tree trunk/plants or males grab females on the ground.

2.7 Secondary reproductives

The term "secondary" is referred to any reproductive individual that is not derived from primary pair(s) (Myles 1999). Generally, "replacement reproductives" are formed when the pair(s) becomes moribund, die or low egg production, in ensuring the continuation of colony's lifespan, while "supplementary reproductives" coexist with the primary reproductives in a satellite colony during a 'budding' process.

Secondary reproductives can develop from both immature apterous and brachypterous castes of termite through one of a variety of potential developmental pathway. For example, apterous castes – larvae, pseudergates and workers give rise to larvoids, pseudergatoids and ergatoids, respectively; brachypterous castes – adultoids and nymphoids derive from alates that retain in the parental colony and nymphs, respectively (Myles 1999). The former group and nymphoids usually lack wing scales and less pigmented. Adultoids resemble primary reproductives, but they are sometimes poorly pigmented and have a pair of torn wing (Leponce et al. 1996). The types of replacement reproductives which develop in any one given colony are highly variable across species, especially in the genus *Nasutitermes* (Roisin and Pasteels 1986a,b, Lefeuve 1987) (Table 2.2) and *Reticulitermes* (Buchli 1956).

In the subfamily Macrotermitinae, only adultoids have been reported (Myles 1999). Myles (1999) divided adultoids into three types: pseudoimagos which show poor

pigmentation and a pair of irregular broken wings, microimagos which possess a pair of shortened wings, and normal adultoids resemble closely to primary imago.

2.7.1 Polygyny

Polygyny is termed as the coexistence of several functional females (queen) in one colony (Schmid-Hempel and Crozier 1999). The phenomenon is widespread in social insects (e.g., ants, bees, termites). Polygyny may happen in termite societies by: (1) a consequence of pleometrosis (several females cooperating during the colony foundation and reproducing actively) (Hacker et al. 2005) (2) budding, especially in polycalic nesting termite species (Roisin and Pasteels 1986b), (3) substituting dead primary reproductives with multiple replacement reproductives (Roisin and Pasteels 1986b, Lenz and Runko 1993).

In view of the benefit to any one colony, the work of reproduction may be shared by several females. This produces a larger worker force, which, in turn, may increase the survival rate of the colonies especially during the early stages of colony development (Thorne 1982, Brandl et al. 2001, Kaib et al. 2001). With several unrelated queen present in colonies may increase intra-colony genetic variability, which allow colonies to be more resistance to disease or parasites and a wide array of extreme environmental conditions (Schmid-Hempel and Crozier 1999). However, competition and conflicts between reproductives to be advance in fecundity and workers' attendance may occur (see section 2.7.2).

Polygyny is common in the subfamily Nasutitermitinae [i.e. *Nasutitermes corniger* (Motschulsky) (Thorne 1983); *Nasutiterms polygynus* Roisin & Pasteels and *Nasutitermes costalis* (Holmgren) (Roisin and Pasteels 1986c); *N. princeps* (Roisin and Pasteels 1986a,b)]. 30% of *N. corniger* colonies contained 2–33 primary queens, while